# Impact of winter ocean warming and reduced heterotrophy on the physiological response of the temperate coral *Oculina arbuscula*

by

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## Abstract

Increasing sea surface temperatures from anthropogenic climate change cause significant stress to marine organisms. A plethora of studies have examined the response of corals to thermal stress under controlled laboratory conditions, which often led to bleaching or mortality of the corals. However, these studies have mainly focused on investigating the response of tropical corals to elevated summer seawater temperatures, leaving a gap in our understanding of how temperate corals are responding to elevated winter temperatures. In this study, we investigated the physiological response of the temperate coral, *Oculina arbuscula*, to end-of-century winter ocean warming and reduced food availability for heterotrophy predicted under climate change. Colonies of *O. arbuscula* were reared for 60 days in two temperature treatments, present-day winter average seawater temperature and elevated winter ocean temperature for predicted end-of-the-century conditions in the northwestern mid-Atlantic region. The corals were also exposed to two feeding treatments of freshly hatched *Artemia* sp. nauplii (low and normal) to examine the effects of heterotrophy on the net calcification rate of the corals. The results of this experiment showed that elevated winter temperatures caused increased calcification rates compared to present-day winter conditions. We also found that heterotrophy has little effect on growth rates for *O. arbuscula.* These findings could have important implications for our understanding of how corals might respond to future climate change effects.

## Introduction

Coral reef ecosystems are an essential resource for humans and marine organisms alike. The complex reef structures created by corals provide habitat and food

sources for marine and terrestrial organisms, protection along the coast from waves and storms, economic benefits from tourism and fishing (Bindoff et al., 2019; Brander et al., 2007), and biodiversity within the oceans (Hoegh-Guldberg et al., 2007). Coral reefs create their calcium carbonate skeletal structures through the uptake of calcium and carbonate ions in the water column via calcification (Drenkard et al., 2013; Rodolfo-Metalpa et al., 2010). Over the past several decades, rates of coral calcification have declined due to anthropogenically-induced global stressors. Anthropogenic carbon dioxide ($CO_2$) absorbed by the oceans is causing a decrease in ocean pH and carbonate saturation states (Drenkard et al., 2013; Ries et al., 2010; Rodolfo-Metalpa et al., 2010; Smith et al., 2016). These effects, together with the formation of carbonic acid from $CO_2$ equilibrating with seawater, is a process known as ocean acidification (Drenkard et al., 2013; Edmunds, 2011; Smith et al., 2016). Additionally, sea surface temperatures (SST) in the 20th Century were on average 0.74 ℃ higher than previous centuries, and temperatures are predicted to continue to increase by up to 4 ℃ by the end of the century (Abram et al., 2019; Hansen et al., 2006; Hoegh-Guldberg et al., 2007; Lord & Whitlatch, 2015). Sea surface temperature is increasing due to atmospheric $CO_2$ amplifying the greenhouse effect (Hoegh-Guldberg et al., 2007). Temperature directly impacts coral calcification rates, and influences both seawater pH and carbonate saturation state, further affecting calcification (Courtney et al., 2017). As a result, coral calcification is expected to continue decreasing due to increased SST and ocean acidification as global climate change persists (Aichelman et al., 2016; Drenkard et al., 2013; Rodolfo-Metalpa et al., 2010).

Corals are mixotrophic organisms, meaning they utilize both autotrophic and heterotrophic feeding to gain the nutrients and energy necessary for growth. Autotrophy

provides carbon to the coral host through photosynthesis carried out by its algal endosymbionts Symbiodiniaceae living within the coral tissue (LaJeunesse et al., 2018; Leal et al., 2014; Smith et al., 2016). Heterotrophy supplements organic carbon obtained from autotrophy, in addition to supplying nutrients, such as nitrogen and phosphorus, needed for tissue growth, symbiont regulation, and reproduction (Smith et al., 2016). Heterotrophy occurs through the capture of dissolved organic matter, particulate organic matter, and zooplankton from the surrounding water column (Aichelman et al., 2016; Leal et al., 2014; Smith et al., 2016). While both of these feeding mechanisms can occur in corals, both methods are not necessary for corals to meet their nutritional demands. In fact, autotrophy can provide up to 100% of a coral's daily metabolic requirements under optimal light conditions (Aichelman et al., 2016; Leal et al., 2014). In particular, scleractinian corals, which are stony or hard corals, display a range of feeding behaviors with some species using primarily autotrophy and others using primarily heterotrophy (Miller, 1995). Corals commonly rely on heterotrophy as a food source more heavily during suboptimal conditions, such as reduced light availability, and many temperate corals utilize heterotrophy in the winter for this very reason (Ferrier-Pagès et al., 2011). During periods of stress, such as those caused by elevated SST, corals bleach, meaning they lose their symbionts and the ability to gain nutrients via autotrophy, thus losing a large portion of their food source (Smith et al., 2016). Bleaching can cause reduced coral health, growth, and reproduction, ultimately leading to coral mortality (Grottoli et al., 2006). Heterotrophy has been shown to increase in bleached corals to maintain metabolism and assist in recovery (Aichelman et al., 2016; Grottoli et al., 2006; Leal et al., 2014; Miller, 1995; Rodrigues & Grottoli, 2007). Several studies have shown that heterotrophy can actually reduce the effects of increasing SST and ocean acidification by minimizing calcification reductions and

reducing harm or loss of symbionts (Aichelman et al., 2016; Edmunds, 2011; Grottoli et al., 2006). Therefore, heterotrophy could offer a possible method for corals to cope with added stress from climate change, but this effect has not been examined in many temperate coral species.

The study organism in this experiment, *Oculina arbuscula,* is a temperate scleractinian coral found in the northwestern and mid-Atlantic Ocean (Aichelman et al., 2016; Leal et al., 2014; Miller, 1995; Ries et al., 2010). It is widespread along the eastern coast of the United States, and establishes a large portion of the benthic hardground shelf ecosystems (Ries et al., 2010), which support economically and biologically important fisheries for the Atlantic Ocean (Aichelman et al., 2016). It is a facultatively symbiotic coral, meaning it does not need symbionts to survive (Aichelman et al., 2016; Miller, 1995). *Oculina arbuscula* is adaptable and tolerates wide ranges of temperature, salinity, and light variations (Miller, 1995; Ries et al., 2010), indicating it will likely be able to survive the changing ocean conditions as a result of climate change. A few previous studies have investigated the impact of heterotrophy on temperate corals, including *O. arbuscula*, under thermal stress (Aichelman et al., 2016; Rodolfo-Metalpa et al., 2010), but none have examined the impact of heterotrophy and winter warming on coral physiological responses. Rather, these previous studies focused on the effect of heterotrophy and rising summer temperatures on *O. arbuscula's* physiological response. Currently, corals grow faster under summer seawater temperatures than winter temperatures (Miller, 1995), but with rising SST, winter temperatures may replace summer temperatures as the optimal growing environment for coral. Higher winter SST may provide better conditions for growth when thermal stress in the summer causes bleaching events and associated reduced calcification rates. Investigation of winter warming would, therefore, help us determine

the impact of seasonal thermal stress, enabling us to better predict how temperate corals are likely to respond to end-of-century winter warming due to climate change.

Additionally, global marine primary production is predicted to decline under current climate change projections, mainly due to increased stratification reducing the supply of nutrients to the upper ocean (Kwiatkowski et al., 2019). Under the business-as-usual Representative Concentration Pathway (RCP 8.5), phytoplankton biomass will decline by 6.1% and zooplankton biomass will decline by 13.6% over the 21$^{st}$ Century (Kwiatkowski et al., 2019). This means heterotrophic food sources available to corals will decrease. In addition, nutrient limitations will decrease phytoplankton nitrogen and phosphorus content relative to carbon levels (Kwiatkowski et al., 2019), leading to trophic amplification as organisms that rely on nutrition from phytoplankton and, thus, the organisms that rely on them, receive less food with lower nutrition. Examining the response of *O. arbuscula* under varying feeding levels is necessary to assess the influence of heterotrophy on coral adaptability. Such findings will help answer important management questions for temperate corals, especially for those that utilize heterotrophy more heavily than other species.

The aim of the current experiment was to investigate the effects of projected winter ocean warming and predicted declines in zooplankton abundance for heterotrophic feeding on the physiological response of the temperate coral, *Oculina arbuscula*. Since *O. arbuscula* is relatively adaptable to temperature and light changes (Miller, 1995), investigating this species allows us to understand how relatively adaptable temperate corals will respond to increasing SST.

## Materials and Methods

### Coral Collection and Maintenance

Fifteen colonies of *Oculina arbuscula* were collected from Radio Island, North Carolina on October 10, 2018 at a 10 m depth using a hammer and chisel. The colonies were transported to the Aquarium Research Center at the University of North Carolina at Chapel Hill. In the lab, the colonies were maintained in two 500 Liter recirculating holding tanks at 22°C, which was the average temperature at Radio Island at the time of collection. Water temperature in the holding tanks was gradually decreased by 1°C per week until they reached 11°C to mimic *in situ* winter seawater temperatures at the collection site. Seawater temperatures were based on data from the NOAA buoy (station BFTN7) most proximal to the collection site to obtain and average weekly temperature records at this location for the past 10 years. The holding tanks were maintained at a salinity of 35 using deionized water and Instant Ocean Sea Salt, which was most similar in chemical composition to natural seawater when compared to other available commercial seawater mixes (Atkinson & Bingman, 1997). The corals were exposed to an irradiance of 150 μmol photons $m^{-2}$ $s^{-1}$, characteristic of low light habitats such as that of the collection site (D'angelo & Wiedenmann, 2012). Mesh sheets were placed on the tank lids for shading to replicate light conditions at the collection site depth. All colonies were fed equal amounts of freshly hatched *Artemia* sp. nauplii once a week (~320 *Artemia* sp. nauplii per mL). Each holding tank had a 50% water change weekly.

Recovery and Acclimation

Each of the fifteen *O. arbuscula* colonies was sectioned into twelve comparatively-sized ramets to ensure that each genet was represented within each treatment level. The corals were sectioned using a diamond-embedded band saw. The ramets were affixed to sterile, prelabeled plastic petri dishes using cyanoacrylate. The ramets were allowed to recover for 30 days before pre-adjustment buoyant weights were measured. The coral ramets were then moved to their separate experimental tanks, with each genet's ramet randomly placed within their respective treatment tank to reduce bias against optimal flow rates and light conditions within each tank. Pre-acclimation buoyant weights were taken. Ramets were then allowed to acclimate gradually to temperatures and feeding quantities based on assigned treatment for 23 days. T0 (time zero) buoyant weights were then conducted at the start of the experiment.

Experimental Design

Twelve 38 Liter experimental tanks were divided into four identical experimental systems, with three tanks in each system. Six of the twelve tanks were assigned to the ambient temperature treatment (average *in situ* temperature at Radio Island) and the remaining six tanks were assigned an elevated temperature treatment (average *in situ* temperature plus 5°C). Within each temperature treatment, three of the six tanks were maintained at low feeding levels (~100 *Artemia* sp. nauplii per mL) while the other three tanks were maintained at ambient feeding levels (~500 *Artemia* sp. nauplii per mL). Therefore, three tanks were maintained at ambient feeding and ambient temperature, three at ambient feeding and elevated temperature, three at low feeding and ambient

temperature, and three at low feeding and elevated temperature. One ramet from each colony was present in each of these twelve tanks so that each genet was represented in all treatments. The experiment was conducted for two months (January 25 through March 25) during most of the winter season in the Atlantic Ocean.

The Apex system was connected to a chiller (AquaEuroUSA Model: MC-1/13HP) for each treatment to maintain constant water temperature within the experimental tanks. The ambient treatment was maintained at ~13°C while the elevated treatment was maintained at ~18°C. Flow rates in the experimental tank systems were maintained at 291 GPH.

Each tank was illuminated with actinic and daylight bulbs (Frequency 50-60 Hz). The lighting was on a 12-hour system with the beginning and end of the period only exposing the corals to actinic light to simulate sunrise and sunset. Corals were irradiated with 150 μmol photons $m^{-2} s^{-1}$ with both the lights on and only 90 μmol photons $m^{-2} s^{-1}$ when the actinic lights were on.

Each of the three 38 Liter tanks in a system was connected to the same 190 Liter sump to recirculate water through the tanks. Each sump had a protein skimmer (Eshopps) to remove organic material, which were cleaned daily. Corals were fed every day to mimic food availability within the water column. The corals received freshly hatched *Artemia* sp. nauplii at least 1 hour after the lights turned off for the day to simulate crepuscular feeding. Ambient feeding conditions were determined from zooplankton abundance averaged from multiple surf zone sites in southeastern North Carolina (8240 individuals per $m^3$) (Stull et al., 2016). This value was used to calculate the quantity of *Artemia* sp. nauplii needed for ambient feeding within the experiment tanks, which was ~500 *Artemia* sp. nauplii per mL. Low feeding was one-fifth of this at

~100 *Artemia* sp. nauplii per mL. Ramets were periodically moved around in the tanks to minimize bias of small flow rate variation that might affect the quantity of food available to a specific ramet.

Experimental Tank Conditions

Salinity was maintained at 35, but often increased in all tanks similarly before each water change due to evaporation. This increase was counteracted through intermittent additions of DI water in all systems until the next water change. Salinity was measured with a refractometer (Cole-Parmer Model: RSA-BR32T) daily. Water changes (33%) were performed twice a week to maintain salinity conditions and reduce excess nutrients. The saltwater mix was cooled to treatment levels using a chiller in order to avoid periods of warmer temperature conditions within the experimental tanks. Water temperature was monitored every day using a glass thermometer while pH was monitored every other day, and adjustments to the tanks were made accordingly. Plexiglass sheets, 3 mm thick, were used as lids on each tank to help minimize evaporation. Tank flow was maintained by pumps (Rio$^{+}$ 2100) within each sump at a flow rate of 2630 LPH. Individual tanks each contained two powerhead pumps (Hydor USA) with flow rates of 240 GPH. Chillers had a flow rate of 291 GPH. Nitrate ($NO_3^-$) concentrations were tested using the Aquarium Pharmaceuticals Nitrate Test Kit (API) weekly to check for excess nutrients building up in the tanks. If build up occurred, a water change was performed.

Calcification Rates and Symbiont Density

*Oculina arbuscula* calcification rates were estimated using a Cole-Parmer bottom-loading balance, following the buoyant weight method (Spencer Davies, 1989).

Coral ramets were buoyant weighed post-recovery, pre-acclimation, at the start of the experiment, every 30 days during the experiment, and at the end of the experiment. Samples were wrapped in aluminum foil and frozen at -80°C at the conclusion of the experiment until lab protocols were initiated. Samples were then thawed for ~10 minutes and tissue was removed via airbrushing with seawater into a Ziploc bag. This tissue slurry was then transferred to 50 mL conical tubes and refrozen until needed for symbiont density quantification.

Dry weights of 45 coral skeletons were measured and plotted against the corresponding sample's final buoyant weight to determine a relationship between the two methods. The relationship was used to determine dry weights for the other coral samples and all buoyant weight measurements taken before and during the experiment.

Surface area of the coral skeletons was obtained using a NextEngine ScanStudio 3D Scanner. The configurational settings used were neutral target, macro range 360 scan with 8 divisions at SD 10K points for scanning resolution. Scans were taken around the axial plane and the coronal plane to get measurements of the full coral sample. These two separate scans were trimmed and then aligned. Once an alignment value of <0.010 was obtained, the scans were fused and polished. The surface area of the whole coral sample was then calculated from the scan and used to standardize the dry weights of each coral sample.

Symbiont density was quantified using the hemocytometer method (Rodrigues & Grottoli, 2007). Briefly, samples were thawed, homogenized, and centrifuged for 15 minutes. Subsamples were taken, and equal volumes of Formalin and Lugol's iodine were added. These were vortexed and counted 3 times from the stained symbiont suspensions on a hemocytometer using a light microscope. These counts were

averaged and normalized to the volume of the tissue slurry and the surface area of the corresponding nubbin.

### Statistical Analysis

All statistical analyses were performed using R software, version 4.0.2 (R Core Team, 2020). Analyses of variance (ANOVA, function anova()) were used to determine the effects of temperature and feeding on the difference in dry weight (normalized to surface area) across each treatment. If factors were found to be significant ($P < 0.05$), post hoc Tukey's HSD tests were used to evaluate the significance of each pairwise comparison.

## Results

### Elevated Winter Temperature Increased Calcification Rates

While many studies have examined how corals respond to warmer summer seawater temperatures, it is unknown how they will respond to the warmer winter temperatures predicted with climate change. We found that calcification rates were significantly higher for *Oculina arbuscula* corals reared at elevated winter seawater temperature compared to corals reared at present-day winter seawater temperature. Additionally, calcification rates were higher for corals reared under low feeding conditions at both present-day winter seawater temperature and elevated end-of-century winter seawater temperature treatment conditions when compared with conspecifics reared under normal feeding conditions (Figure 1).

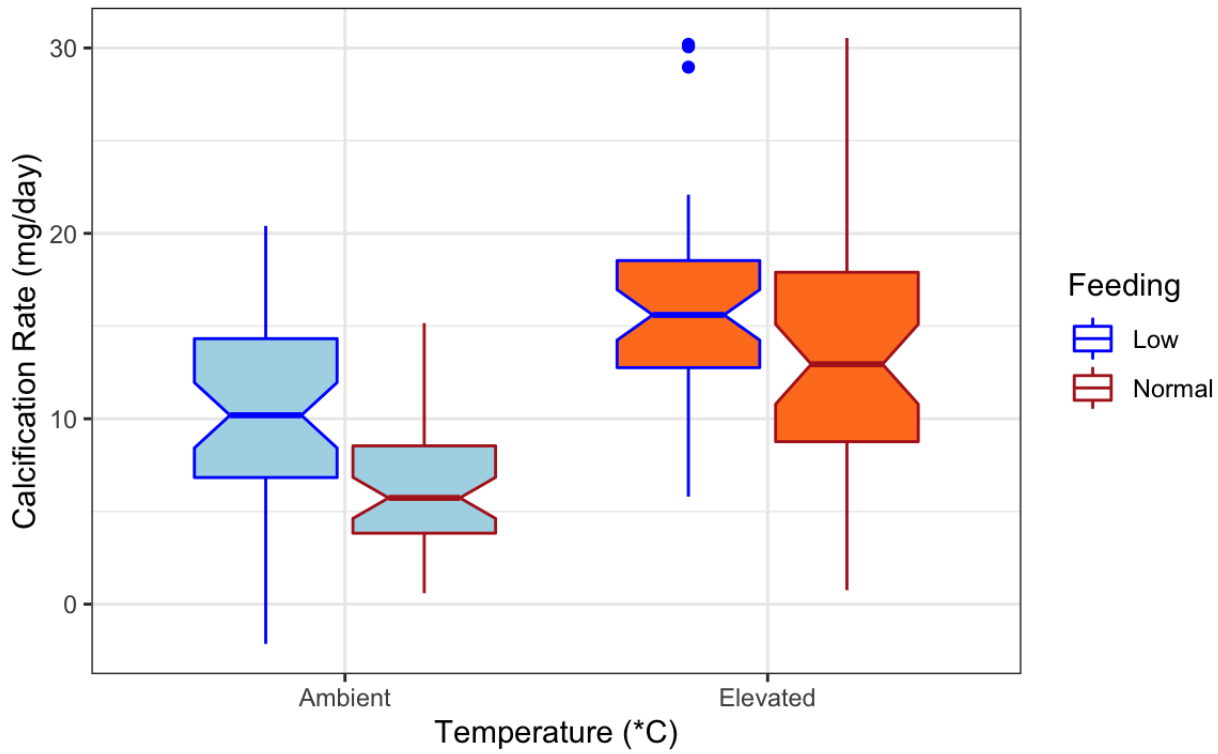


**Figure 1**. Effect of winter temperature on calcification rate of *Oculina arbuscula* at low and normal feeding treatments. Notches represent 95% confidence intervals (n= 45 samples per treatment).

Calcification Rates Were Positive Over Each Experimental Interval

Over both observational intervals (i.e., 0-30 days and 31-60 days), corals reared at warmer winter temperatures exhibited higher calcification rates regardless of feeding treatment. In addition, corals in all treatments maintained calcification over the first 30 days of the experiment and this consistent calcification trend persisted through the end of the experiment (Figure 2).

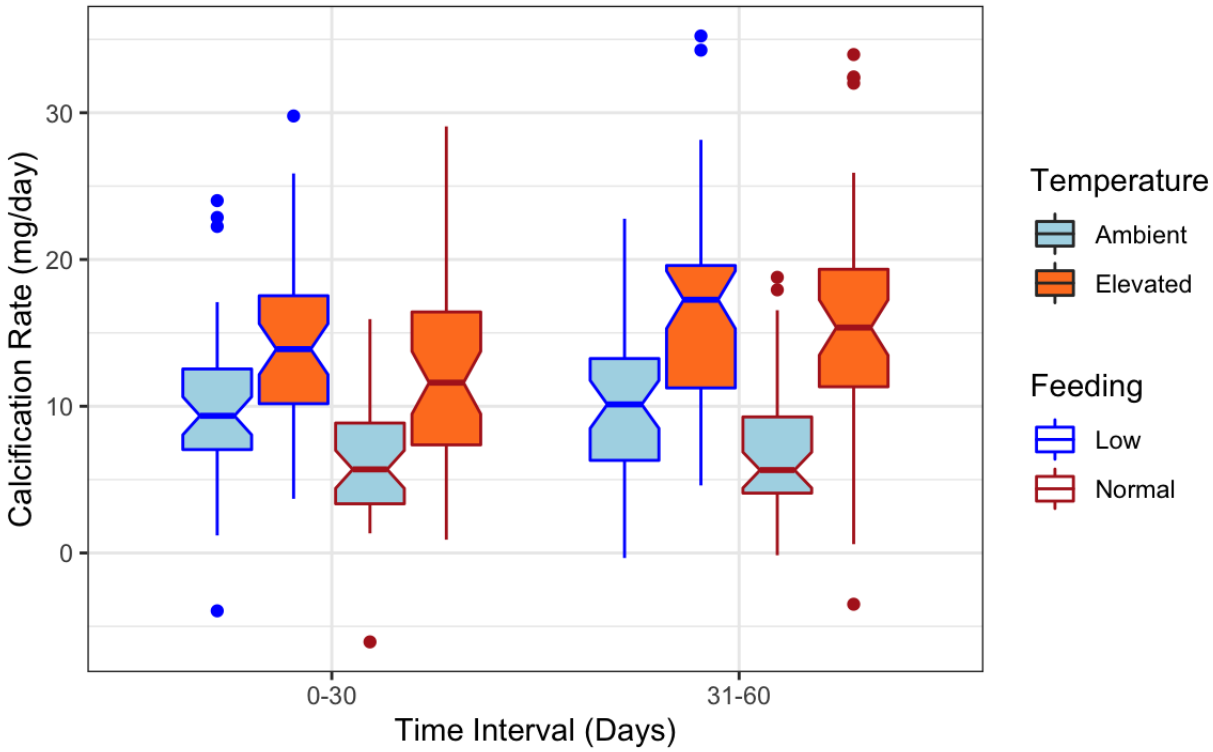


**Figure 2.** Effect of winter temperature on calcification rate of *Oculina arbuscula* for each treatment over 30-day intervals (n= 45 samples per treatment).

## Discussion

Elevated winter temperatures offer potential advantage to corals for winter calcification rates

This experiment shows that *Oculina arbuscula* calcified at a greater rate under future elevated winter temperatures than at current seawater temperatures. The difference in dry weight change between the ambient and elevated temperatures for both low and normal feeding conditions was significant, indicating warmer temperatures benefit the corals' calcification rates. This is likely due to higher metabolic rates at warmer temperatures since *O. arbuscula* is known to grow four times faster in the summer than during the winter (Miller, 1995). Additionally, current seasonal temperature changes result in undersaturated aragonite concentrations in the ocean during the

coldest period of the year (Ries et al., 2010), meaning corals have less aragonite to perform calcification during the winter. Elevated winter temperatures would likely mean increased aragonite saturation, enabling corals to calcify more in these conditions. Therefore, increased aragonite availability, along with a higher metabolic rate from warmer winter temperatures, could explain why *O. arbuscula* had higher rates of calcification in the elevated winter temperature treatment.

Heterotrophy has little impact on calcification rates

Heterotrophy appears to have no benefits to calcification rates in *O. arbuscula* for either temperature treatment, and even potentially hinders calcification since corals at low feeding conditions grew faster in both temperature treatments than corals reared at normal feeding conditions. This indicates that *O. arbuscula* likely relied more heavily on its symbionts for nutrition than on heterotrophic food sources. *Symbiodinium* type B2, now genus *Breviolum* (LaJeunesse et al., 2018), is the only symbiont present in *O. arbuscula*. This symbiont is physiologically tolerant to cold stress and rapidly recovers from prolonged exposure, functioning minimally at temperatures as low as 10°C (Thornhill et al., 2008). Since the treatment temperatures were above this lower threshold, *Breviolum* was actively photosynthesizing to provide nutrition to the coral, allowing it to calcify under the winter conditions. Therefore, autotrophic food sources played a larger role in the calcification rates of *O. arbuscula* than heterotrophy.

Implications for future climate change predictions

In the temperate coral *O. arbuscula*, Aichelman et al. (2016) found that under summer thermal stress, greater net calcification occurred in corals fed heterotrophically

than in those unfed, indicating heterotrophy can mediate the negative effects of temperature stress on calcification. In the predicted elevated winter temperature used for this experiment, *O. arbuscula* exhibited greater net calcification regardless of heterotrophic feeding levels. This suggests that the winter season may become the optimal time for growth under future climate change conditions as corals do not appear to exhibit a stress response during periods of warmer winter seawater temperatures. If corals continue to grow more quickly during the winter from these elevated temperatures, this may allow for a large portion of recovery from the effects of thermal stress in the summer to now occur in the winter. Together, these responses may lead to a shift in the seasonal pattern of coral growth with the winter becoming the main period for growth and the summer shifting to an inactive period so corals can survive the added stress from summer thermal events predicted with climate change.

## Conclusion

Although many studies evaluated how heterotrophy affects corals under summer thermal stress, none have looked specifically at the effects of elevated winter warming on temperate corals. This study aimed to understand how *Oculina arbuscula* responds to winter warming and if heterotrophy played a role in its physiological response. The results of this experiment show that heterotrophy did not impact calcification rates of *Oculina arbuscula*, but rather that elevated winter temperatures cause faster growth during the winter season. Future studies should focus on the relationship of summer and winter thermal stress to understand the response of *O. arbuscula* on a yearly scale.

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